

The University of Chicago

DEVELOPMENT AND STRUCTURE
OF THE WATERMELON
SEEDLING

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1937

By

GAYLE N. HUFFORD

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DEVELOPMENT AND STRUCTURE OF THE WATERMELON SEEDLING

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 493

GAYLE N. HUFFORD

(WITH FORTY-NINE FIGURES)

Introduction

BARBER (1) studied the fruits and seeds of the watermelon, *Citrullus vulgaris* Shrad. In addition to histological investigation, she determined that the cells of the embryo contain oil and protein granules as reserve food. Later, LANGELD (7) compared the oil content of seeds of various crop plants and found that those of watermelon were highest in this respect, ranking above those of pumpkin and soy beans. Using root tips as material, WHITAKER (12) determined the chromosome number of several of the cultivated Cucurbitaceae. He reported eleven as the haploid number for *Citrullus*. CROCKER and associates (2) considered the peg to be a local overgrowth of the cortical cells, and demonstrated that such overgrowth is stimulated mainly by the arching of the hypocotyl. HOLROYD (4) made comparative histological studies of several of the Cucurbitaceae, particularly of the mature stems. He described *Citrullus* as "excelling all other members of the family in length of axis, luxuriant growth of side branches, and in size of hypocotyl and immediately connected regions above and below." He also considered the sieve tubes to be the largest of any cucurbits studied, those of the external phloem averaging twice the size of those of the internal. SLEETH (11) has shown that the formation of tyloses in *Citrullus* is incited by *Fusarium nivium*. Plants one to four months old showed an abundance of tyloses, the abundance being correlated with the quantity and nearness of the fungus. The evidence indicates that the formation of tyloses precedes or coincides with the spread of the fungus through the xylem. HOLROYD (4) and RUTLEDGE (10) have reviewed the extensive literature dealing with the nature of the bicollateral bundles in the Cucurbitaceae.



It is the purpose of this investigation to show some of the developmental and structural features of the early stages of the seedling.

Material and methods

Plants were grown in the field and in the greenhouse, and very young seedlings were germinated in moist cotton. Since the peg normally causes the hypocotyl to emerge at a sharp angle with respect to the primary root, it is difficult to obtain strictly transverse serial sections in the transition region. This difficulty was overcome by germinating the seeds in an erect position, micropylar end downward, and with the seed coats partially removed after the general method used by CROCKER (2). Most seeds so prepared were germinated in moist cotton, since it was easier to secure and maintain an erect position by wrapping the seeds in moist cotton pads and inserting the pads in shell vials. Some seeds so prepared were also grown satisfactorily in the greenhouse.

The best results for all young tissues were obtained when they were fixed in a Navashin solution made up as follows: (A) 10 cc. glacial acetic acid, 1.5 gm. chromic acid, and 90 cc. distilled water; (B) 40 cc. formalin and 60 cc. distilled water. Equal amounts of the two solutions were mixed just before using. Older tissues were fixed in formalin-alcohol.

Chloroform was used to clear all material to be sectioned. Cedar oil was used to clear seedlings for macroscopic study of the vascular system. Seedlings for this purpose were killed in formalin-alcohol and left in the solution until the chlorophyll had been dissolved from the tissues. They were then split along one side of the hypocotyl to the pith cavity, laid open, and clamped between two microscope slides. So held they were dehydrated in alcohol and cleared with cedar oil. Serial sections for the study of histogens of the root were cut at 6μ ; all others at 12μ . Flemming's triple stain was used.

Investigation

GERMINATION AND SEEDLING

The mechanics of germination are practically identical with those described by CROCKER (2) for other Cucurbitaceae. After the emergence of the primary root, the peg forms rapidly, so that by

the time the root is 2-3 cm. long it has fastened itself firmly against the lower half of the seed coats, while the simultaneous arching of the hypocotyl splits the halves apart. The opposing pull of the hypocotyledonary arch against the peg pulls the cotyledons from the integuments. These are left beneath the soil, often clamped over the peg. Rapid growth of the lower hypocotyl forces the arch upward through the soil and above ground. Continued growth results in the cotyledons being rapidly pulled from the soil. The arch straightens out and the cotyledons spread apart. Although yellowish or white at the time of emergence, the cotyledons and the aerial portions of the hypocotyl develop chlorophyll. It is only when seeds are planted on the micropylar end that the seed coats are carried above the ground by the cotyledons.

The time required for germination varies greatly. The seeds are very sensitive to temperature and water conditions. In warm greenhouse conditions the radicle usually emerges within 36-48 hours, and the cotyledons will be out of the ground and spread apart within four days. Growth of the hypocotyl is rapid. Within eight to ten days from time of planting it will have attained a length of 9-11 cm., which is about its maximum in an optimum environment. During this time there is a correspondingly rapid growth of the primary root and its branches, and of the cotyledons. The latter are ovate and have long and short diameters of about 11 and 7 mm. at the time they appear above the soil. Within a few days they reach maximum size, the average long and short diameters being 4 and 2 cm. respectively. These data relate to greenhouse-grown plants; under field conditions the periods of growth will be lengthened in proportion to the departure from optimum atmospheric conditions.

Full expansion of the cotyledons marks a definite stage in the growth of the plant, since two weeks to a month may elapse before further appreciable lengthening of the axis occurs. This stage is arbitrarily referred to as the seedling, of which this study covers only the earlier stages; that is, before marked secondary thickening has taken place.

At the time the cotyledons first spread apart the epicotyl is hardly visible. The point of the first regular leaf is deeply set in the angle between the cotyledons. The latter are densely spinulose

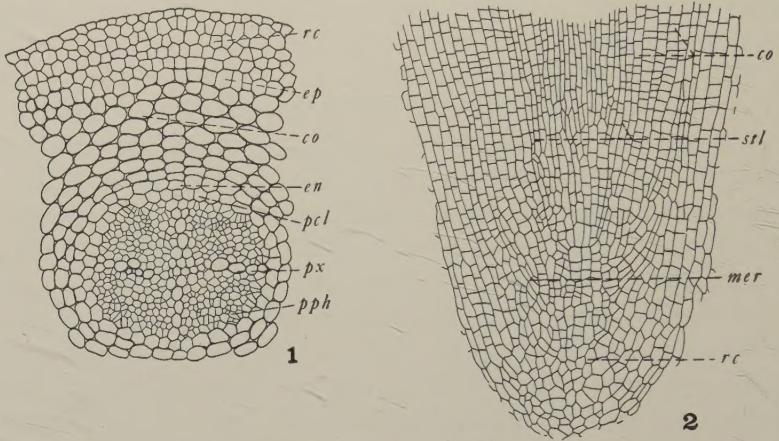
above and glabrous beneath, and each has seven main veins, more prominently displayed on the lower surface. The hypocotyl is somewhat flattened in the plane of the cotyledons and tapers slightly as it approaches them. It ranges from 3 to 4 mm. in diameter just above the peg to 1-1.5 mm. just below the cotyledons. Its surface is beset with spinulose hairs which increase in number and size from the ground upward. The primary root grows rapidly and apparently continues to do so throughout the life of the plant. It tapers abruptly just below the peg, and from it arise many laterals, definitely four ranked.

PRIMARY ROOT AND TRANSITION

The primary root is tetrarch exarch. Its general organization is evident early in the ontogeny of the axis. Figure 1 shows a transverse section less than 1 mm. from the tip of a very young seedling in which the primary root had attained a length of approximately 5 mm. The protoxylem has begun to differentiate and shows as a cross within the pericycle. The primary phloem is somewhat more advanced in its development. In fact it is characteristic that the phloem precedes the xylem in development, and also exceeds it in amount formed. The pericycle is uniformly one cell thick opposite the phloem, except that there is usually an extra layer two to four cells wide adjacent to the protoxylem. The cells of the pericycle are large and angular in cross section. The endodermis can be determined by position only, since its cells approximate the size and shape of the cortical cells. No Casparian strips are visible. The cortex is from eight to ten cells thick. The cells are very large, oval, and somewhat compressed periclinally. The intercellular spaces are many. The epidermis is composed of one layer of cells, which are more or less rectangular in cross section. Around the epidermis at this level there are four or five layers of the root cap which have not been abraded. The cells resemble those of the epidermis, and compactly surround them. With the exception of the outer cap cells, all are highly meristematic, as is evidenced by their thin walls, prominent nuclei, and dense cytoplasm. The protoxylem is becoming definitely differentiated.

Figure 2 shows a median longitudinal section through the root

tip. As indicated, there are no definite histogens. At the apex is a common meristematic region from which all tissues are derived. This meristem lies in a horizontal plane at the base of the central cylinder, but outward from the cylinder it is turned up slightly, so that it has the shape of a shallow bowl. All stelar and cortical tissues are derived from cells cut off to the inside of this bowl-shaped promeristem. Cells cut off to the outside form the calyptra. Cells are cut off centripetally from the upturned edges of the meristem.



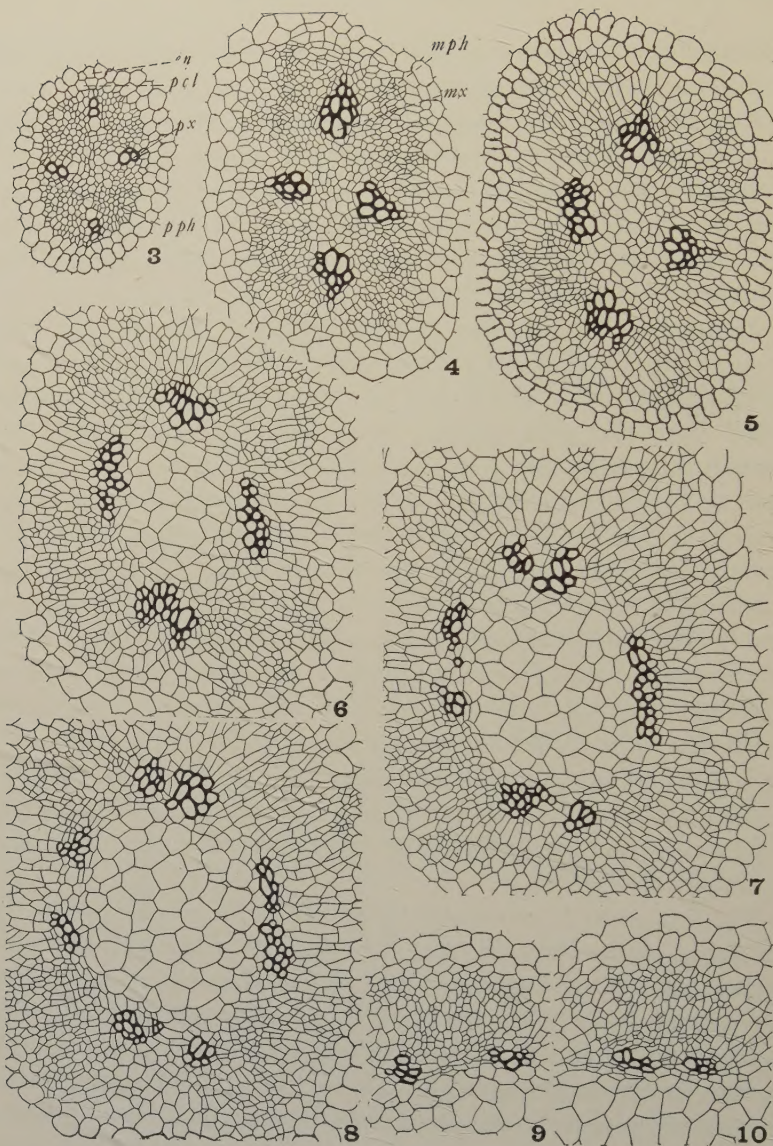
FIGS. 1, 2.—Sections from meristematic region of primary root: Fig. 1, cross section 2 mm. back from tip showing early differentiation of tissues (*rc*, root cap; *ep*, epidermis; *co*, cortex; *en*, endodermis; *pcl*, pericycle; *px*, protoxylem; *ppsh*, protophloem). Fig. 2, median longitudinal section through tip showing nature of unorganized meristem (*stl*, stele; *mer*, meristem). $\times 27$.

Because of this the cap does not break away from the root, but adheres closely to it for considerable distance. Continued, although irregular, breaking away of the cap cells eventually leaves the innermost layer of these cells, which were cut off externally from the meristem, as the epidermis. As a consequence of its irregular method of derivation, the epidermis usually presents a rather uneven surface instead of the smooth and even surface of an epidermis derived from a definite dermatogen. This meristematic region of *Citrullus* is similar although not identical with the type of meristem described by JANCZEWSKI (5) as being common among the Cucurbitaceae and the Papilionaceae. He considered the upturned outer limits of the

meristem the transverse generating layer from which the central cylinder and the cortex are derived to the inside, and the calyptra to the outside. He also described the manner in which the epidermis is developed. The description given thus far relative to figures 1 and 2 applies to the tip region regardless of the age or the length of the root. In slightly older roots, 15–20 mm. long, it is possible to follow the development of the primary root by examining identical structures at successively higher levels.

Figure 3 shows a section about 8 mm. back from the tip. The protoxylem is well differentiated, being composed of annular and spiral elements. The metaxylem has begun to differentiate centripetally from the protoxylem. The primary phloem shows little greater differentiation. The elements of each of the four groups tend to be divided into two smaller groups toward the adjoining protoxylem points, with prominent parenchyma cells between each group. There is no marked change in the pericycle. The endodermis is well marked by Casparian strips, which are more prominent here and in immediately adjoining regions than at any other level. There are no further changes in the cortex or epidermis, except increase in length. The length of each cell eventually becomes eight to ten times its width. Ultimately both are abraded. This loss begins early and proceeds gradually and irregularly. Apparently no cortical periderm is formed. Study of mature roots indicates that a periderm is formed by the pericycle as it becomes exposed by the final disappearance of the cortex.

Figure 3 shows a section still higher up, about 10.5 mm. from the tip and 4.5 mm. from the peg. The primary xylem has been augmented by the maturation of metaxylem elements centripetal to the protoxylem, which shows signs of being crushed out. The metaxylem consists of tracheids and large scalariform and scalariform-reticulate tracheae. There has been considerable addition to the primary phloem by the continued differentiation and maturation of metaphloem. Its elements are somewhat more specialized, sieve tubes and companion cells being present in addition to parenchyma. No crushing of the primary phloem was observed in any seedling material. In this respect, the functional persistence of the primary phloem, the situation is apparently similar to that reported for the

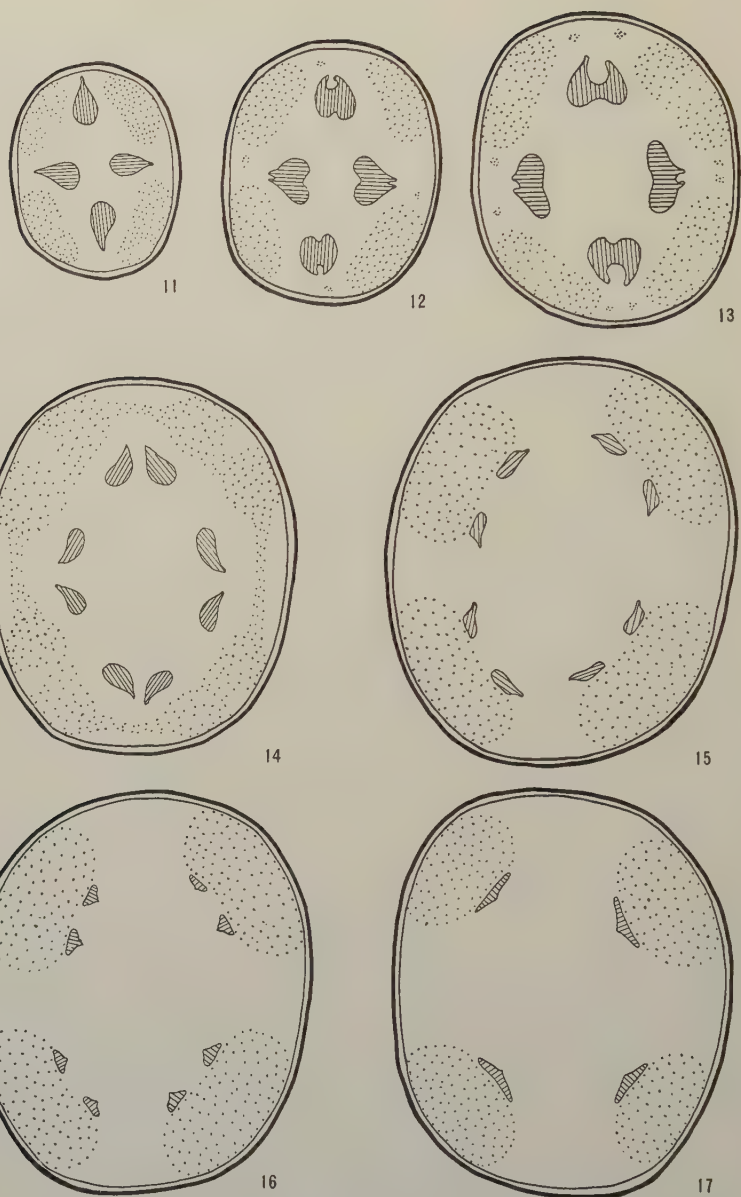


FIGS. 3-10.—Transverse sections from primary root about 15 mm. long showing differentiation of metaxylem and metaphloem and critical stages of transition. Figs. 3-5, stele and endodermis; figs. 6-8, stele, including pericycle; figs. 9, 10, one transition bundle only (*en*, endodermis; *pcl*, pericycle; *px*, protoxylem; *p ph*, protophloem; *mx*, metaxylem; *m ph*, metaphloem). $\times 27$.

genus *Cucurbita* (3). The pericycle of this and of succeeding levels is irregularly one to three cells thick, the extra layers being particularly noticeable opposite the protoxylem. Casparian strips are still prominent. The pith is more extensive than at lower levels, owing more to the increase in size of its cells than to their increase in number. The pith is present throughout the length of the primary axis. The combined proliferations of the various tissues and the growth of cells have practically doubled the width of the stele at this level as compared with the one just described. This rapid flaring of the primary root continues up to its merge with the hypocotyl at the level of the peg.

Figure 5 represents a section 2.5 mm. above the one just described. The most notable change in the primary xylem is the much greater width of each of the four groups, due to continued differentiation of metaxylem laterally. There is evidence that each xylem group is about to diverge radially into two groups. The phloem groups are also much wider, owing to the greater number of parenchymatous cells between the smaller units within each large group. Small clusters of phloem elements are also sparsely scattered in the rays opposite the xylem. Sieve tubes and companion cells are well differentiated in the phloem at this level. The Casparian strips are not so distinct, being most prominent opposite the phloem.

Beginning here also there is rapid reorientation of the vascular bundles from the exarch and radial alignment of the root to the endarch and collateral alignment of the stem (figs. 11-17). First there is a radial separation of each xylem group to form two groups. These new groups apparently are diverged with the metaxylem ends turned away from each other and swung centrifugally through arcs of 180° . At about the time the protoxylem is lateral in position, the two sub-groups of phloem within each large group are far enough apart exactly to subtend the reoriented groups of xylem. This divergence of the phloem is sufficient to separate, almost if not quite, each phloem group into two distinct groups. At this time there are apparently eight bundles, therefore, but these are evidently in four closely aligned pairs. The continued lateral development of the xylem groups results in the members of each of the four pairs coming together to form four endarch collateral bundles, com-



FIGS. 11-17.—Diagrammatic drawings, based on figs. 3-10, showing nature of transition. Outer heavy line represents endodermis; inner line, pericycle; dotted areas, primary phloem; and lined areas, primary xylem.

pleting transition. Finally there are as many bundles as at the beginning. The phloem of each new bundle is that of one of the original groups, while the xylem is related to two bundles, half of each being continuous with the lateral half of two of the original bundles. These two strands maintain their entity for a time, but there is less parenchyma differentiated between them so that there is soon but one compact group. This final alignment of the four endarch bundles occurs at the lower level of the peg, scarcely 2 mm. above the level of the beginning of transition.

There are other important histological situations in the transition zone which are not particularly related to transition itself. These are indicated in the diagrams and in the detailed drawings made of sections taken at critical levels. Figures 12-14 show the presence of phloem across the rays opposite the xylem, while figures 15-17, taken at higher levels, do not show it. Figures 3-10 are of corresponding portions, as indicated in the diagrams. More and more sieve tubes and companion cells, separated by small groups of parenchyma, are differentiated, so that eventually there are no rays, but a continuous band of phloem. This is of considerable physiological importance, since it gives every portion of the root a connection with food channels so long as even one bundle retains its food conducting ability. A second important fact is that the tissues in the upper transition regions (at peg level) are more juvenile or nearer the embryonic condition than are those farther down the axis. This is particularly noticeable in the relative maturity of the xylem elements. This retention of meristematic activity is related to the rapid growth of the lower portions of the hypocotyl, especially during germination.

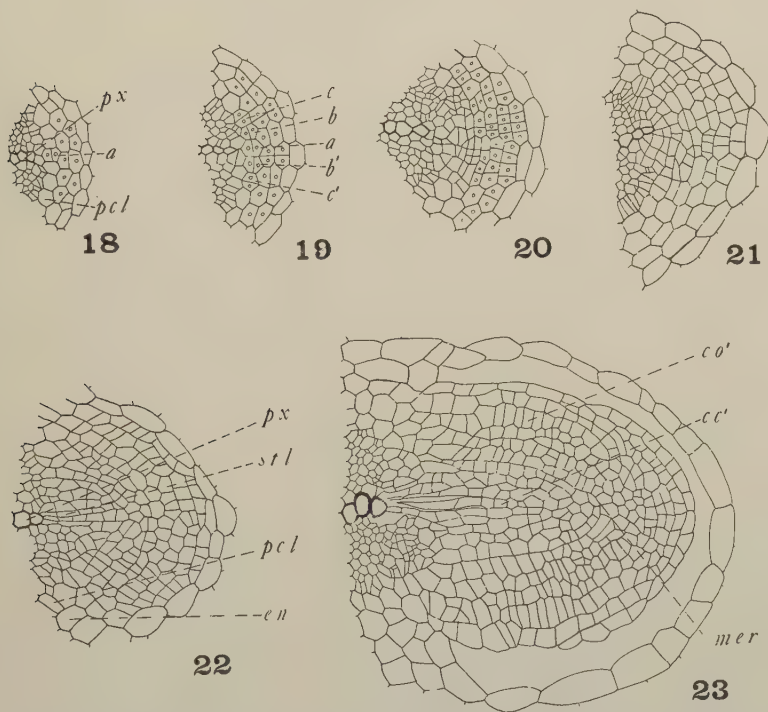
ORIGIN OF SECONDARY ROOTS

In addition to the abundance of secondary roots, they are characterized by their very early appearance from the viewpoint of ontogeny, and by the unusual manner of their origin. In general, the manner of origin agrees with that described by JANCZEWSKI (6). LE MAIRE (8) confirmed the work of JANCZEWSKI and elaborated somewhat on the mechanics of development in the different types of origin of secondary roots. Both considered this particular type

to be peculiar to the cucurbits and the legumes; both agreed as to the general plan of development; and both found considerable difficulty in tracing the exact procedure because of the tardy differentiation of primary tissues in the secondary roots. They concluded that the origin and nature of the meristem of the secondary root is as unusual as that of the primary root. Briefly they characterized this type as follows. Only the central cylinder of the secondary root arises from the pericycle of the primary; the remaining tissues are derived from the endodermis and the inner layers of the cortex.

Figures 18-23 are from cross sections of the primary root taken from levels successively back from the apical meristem, and are selected to show the activities of various tissues of the primary root in the development of secondary roots. Figure 18 shows a single cell of the pericycle which has divided tangentially. It is exactly opposite a protoxylem point. At the time this division occurs the protoplasm is dense within the adjoining cells of the pericycle, as well as in the surrounding cells of the endodermis and proximal cells of the immediately adjoining cells of the cortex. Figure 19 shows cells on either side of the initial divided, also tangentially, while the one next to each of these has divided radially. These two cells, which divide radially, mark the limits of the pericycle which enters into the formation of the secondary root. In addition several cells of the endodermis have divided tangentially, and some of the cells so derived have divided radially, thus outlining the beginnings of the secondary root in the cortex of the primary. Likewise radial divisions have occurred in the two or three layers of pericyclic cells previously mentioned as occurring opposite the xylem points. JANCZEWSKI (6) refers to these inner cells, together with those of the main layer of the pericycle, as pericambial, because of their relation to the formation of secondary roots. Figure 20 shows continued proliferations of all the tissues and also divisions beginning to occur in an adjacent layer of the cortex. Figure 21 shows, in addition to continued divisions, the beginning of demarcation of the central cylinder of the lateral root. In figure 22 this demarcation is still more definite. The stele of the secondary root is also accentuated by cells which form the xylem connections between the secondary root and the

xylem strand opposite which it is formed. Here too is evidence of the formation of the terminal meristem of the lateral root. Because



FIGS. 18-23.—Cross sections from primary root showing development of secondary roots: Fig. 18, single cell (*a*) of pericycle divided transversely to become a secondary root initial; other nucleated cells are results of divisions of endodermal cells (*px*, protoxylem; *pcl*, pericycle). Fig. 19, two pericyclic cells (*b*, *b'*) adjoining the initial have divided tangentially and two cells (*c*, *c'*) adjoining these have divided radially; all other nucleated cells still of endodermal origin. Figs. 20-21, continued development of secondary root tissues through proliferations of pericyclic and endodermal tissues. Fig. 22, stele of secondary taking form and inner cortical layers of primary contributing to outer tissues of secondary (*pcl*, pericycle of primary; *en*, endodermis of primary; *co*, cortex of primary; *stl*, steler tissues of secondary). Fig. 23, secondary ready to emerge through last cortical layer of primary (*cc'*, central cylinder of secondary, developed from pericycle of primary; *co'*, cortex of secondary, developed from endodermis and inner cortex of primary; *mer*, developing meristem of secondary). $\times 35$.

of the extent to which various tissues of the primary root have contributed to the formation of the secondary, it is difficult to recognize

with exactness the origin of the terminal meristem of the latter. JANCZEWSKI assumed that finally it is derived partly from the terminal cells of the central cylinder and partly from the cells, of endodermal origin, which surround the tip of the central cylinder. I was unable to determine from the material studied the exact origin of the cells in this meristematic region. From such as were examined, as illustrated in figures 22-23, such an opinion seems valid. Apparently a considerable portion of this tissue is of endodermal, and perhaps cortical, origin. Figure 23 shows the lateral root just ready to emerge from the primary. It shows the extent to which the endodermis and cortex have contributed to the building up of the tissues of the secondary roots. There is little or no solution and resorption of the primary cortex as the secondary root penetrates it. Subsequent derivation of cells of the lateral root is from its meristem, which, according to JANCZEWSKI, functions similarly to that of the primary root.

PEG

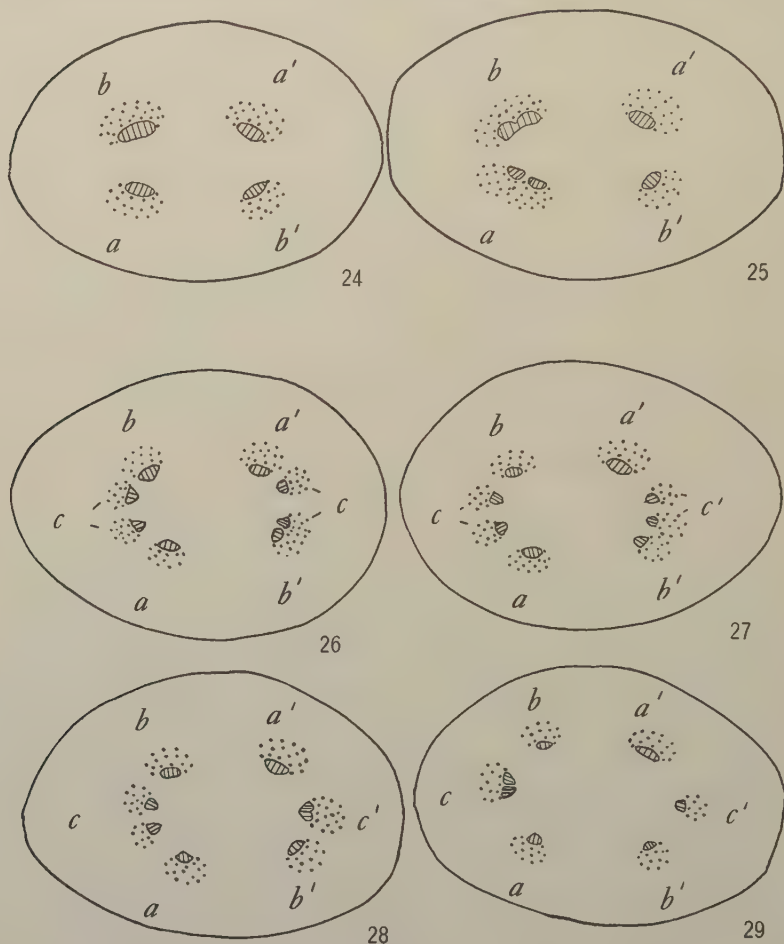
The peg is located on the axis exactly at the level of transition. Spinulose epidermal hairs, characteristic of the hypocotyl, occur on the upper face of the peg, and root hairs on its lower face. Since the peg has been adequately described by CROCKER and others (2) for other genera of the Cucurbitaceae, and since no variation from their findings was found in *Citrullus*, no detailed discussion is deemed necessary here. The most pronounced development of a peg occurs when seeds are germinated in a flat position. In such position the cortical cells composing the peg have their longest diameter in a radial plane, whereas elsewhere their longest diameter is in the vertical plane. There are also more layers of cells across the cortex at the peg than are found elsewhere in it. That it may appear at any radius or on opposite sides, in the case of seeds planted in an erect position, indicates that the peg is a localized cortical structure developed in accordance with the direction of the stimuli which initiate it.

HYPOCOTYL

As previously stated, the hypocotyl is flattened in the plane of the cotyledons. At its lowest level, about where transition is com-

pleted, there are four transition bundles. These are not uniformly spaced but are paired, with more space between the pairs than between the two bundles of a pair. This spacing of the bundles is associated with the flattening of the hypocotyl. Following transition, divergences occur in all, or at least in two, of the four bundles. Usually branches diverge from each of the two bundles which are paired toward the ends of the oval as seen in cross section. These branch bundles always come from the sides of the bundles facing each other, so that they are at the ends of the oval. They move together rapidly, and anastomose at levels varying from 1 to 5 mm. above the peg. There is some variation. Sometimes only one of each of the paired bundles branches and sometimes two of one pair may branch and only one of the other pair. In most cases both of the pairs branch. In all cases, when the process has been completed there are six bundles, now so spaced as to appear as two sets of three at opposite ends of the oval. Figures 24-29 are of transverse sections taken from successively higher levels in this zone, and show how the six bundles of the hypocotyl arise from the four transition bundles. Figure 30 is a schematic drawing made from cleared specimens showing the same features and also the xylem in transition. In many cases the bundles of the hypocotyl continue as six up to the cotyledons. In other cases additional branching may increase the number to eight. These two additional branches are also divergences from one or more of the original transition bundles. They are always from the side of the bundle opposite that from which the first branching occurred, and lie along the sides of the oval as seen in cross section. Apparently these two new bundles may come from any of the four but they are always on opposite sides of the hypocotyl, evidently providing food channels through the extensive tissues lying between the sets of bundles already present. Moreover there is no fixed level at which they diverge. Sometimes one or both may appear near the base of the hypocotyl; more commonly they appear higher up. In the region just below the cotyledons, the branch bundles lying along the flattened sides of the hypocotyl, provided such branches have formed, anastomose with one of the parent bundles between which they lie. Usually such a branch is reunited with the bundle from which it is diverged. In a few cases

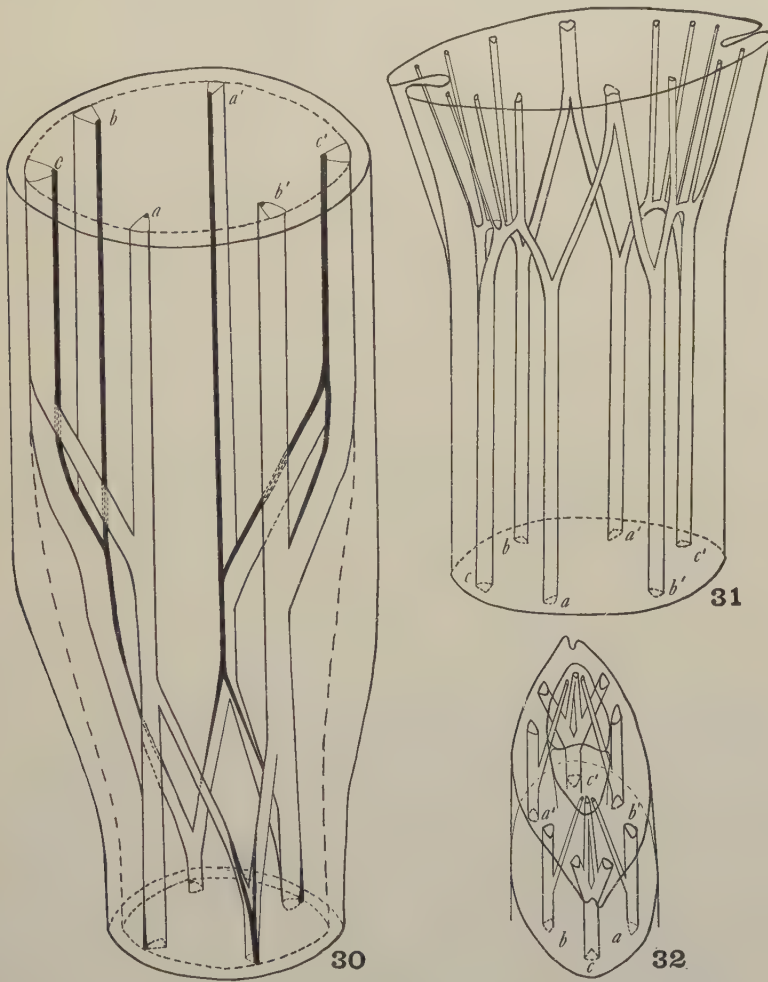
it is separated into two strands, one going to each of the two bundles between which it lies. In all cases observed this anastomosing again reduces the number to six, at or below the level at which they



FIGS. 24-29.—Diagrammatic drawings of cross sections from lower hypocotyl showing origin of six bundles of hypocotyl from four transition bundles. *a*, *a'* and *b*, *b'* are opposite transition bundles; *c* is formed of anastomosing branches from *a* and *b*, while *c'* is likewise developed from *a'* and *b'*.

enter the cotyledons. Because very often there may be no more than six bundles in the hypocotyl, and because the additional bundles, if present, are irregular as to the levels at which they occur and

always anastomose with the parent bundles, six bundles are considered the typical number, as shown in all illustrations. The



FIGS. 30-32.—Schematic drawings showing general plan of vascular system: Fig. 30, root stem transition (below) and organization of six bundles of hypocotyl from four transition bundles (above). Fig. 31, manner in which hypocotyledonary bundles pass into cotyledons. Fig. 32, vascular connections to epicotyl. Bundles lettered throughout as in figs. 24-29.

bundles are bicollateral throughout the length of the hypocotyl. There is considerably more external phloem than xylem, so that it

extends far around the xylem group in each bundle. The rapid differentiation of phloem soon provides a striking preponderance of phloem. The various elements within the bundle are similar to those of the root. Figures 47-49 show these features of typical hypocotyledonary bundles. There is no interfascicular cambium. Consequently all thickening, aside from the small amount accomplished by fascicular cambium, is owing to activity of the parenchymatous tissues. This feature was reported by POTTER (9).

The epidermis is composed of greatly elongated and flattened cells. It is richly supplied with stomates.

The cortex is like that of the root except that the cells become even longer, and are filled with chloroplasts to considerable depth. The endodermis and pericycle are irregular and indistinguishable as a rule. It is possible to trace the pericycle.

The central pith begins to disintegrate early throughout the length of the hypocotyl. Such disintegration is limited to the larger cells in the central region; the outer portions of the pith remain intact and are parenchymatous, especially in the region of the bundles.

COTYLEDONS

All bundles of the hypocotyl terminate in the cotyledons. There are five main bundles at the base of each cotyledon, the three centrally located ones being very prominent. In addition to the five there is a smaller branch bundle at each edge of the cotyledon. These seven form the primary framework of the whole structure. This bundle alignment is derived from the six bundle arrangement of the hypocotyl (figs. 33-44, 31). The tapering of the hypocotyl toward the top amounts almost to a constriction at the level of divergence of the cotyledons. In this region the three bundles located in each of the two ends of the oval, as seen in the cross section, are so close together as to form apparently one large bundle, in which, however, the three bundles maintain their identity. A cross section at this level (fig. 36) shows these two semicircular bundle groups with prominent rays between. At the same time the two bundles in the ends of the oval, the last formed of the six hypocotyledonary bundles, begin to divide into two separate

bundles. Immediately these, and likewise the other bundles, move outward from the semicircles toward the rays. When the separation is complete there are four bundles along each side of the oval. The two inner ones on each side are the original four transition



FIGS. 33-44. Transverse sections from upper hypocotyl showing divergence of hypocotyledonary bundles into cotyledons and vascular connections to epicotyl.

bundles, by position at least, while the two outer ones are branches from the bundles lying in the ends of the oval and formed by the anastomosing of strands from the original four. The two inner bundles of the four on each side continue to move toward each other

and finally unite to form the midribs of the two cotyledons. The outer two bundles of each cotyledonary group branch and thus increase the number to five, and this number is soon increased to seven by the smaller branches which again diverge from the outermost bundles. All the bundles of the cotyledons are loosely joined by archlike connections (fig. 31) which are produced in the apparent moving together of the hypocotyledonary bundles to form the semicircles. For the most part, these connections are composed of phloem tissue.

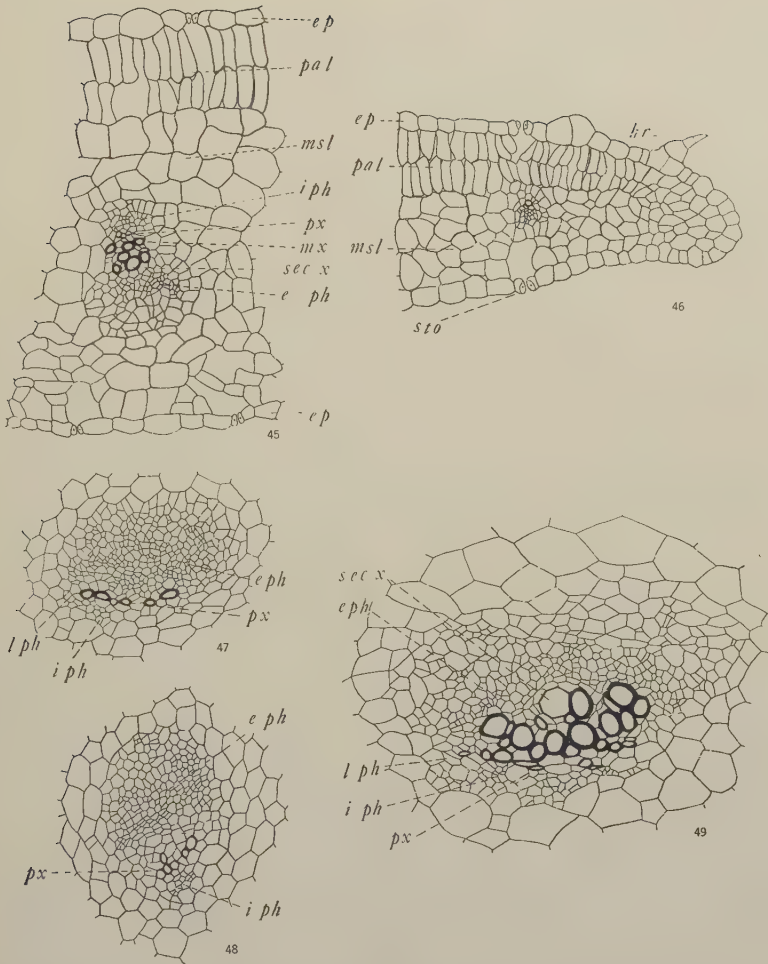
Simultaneously with establishment of their vascular framework, the cotyledons also diverge from the axis. The epidermal cells are very irregular in shape and size, presenting a mosaic-like surface view characteristic of many dicotyledonous plants. Stomata are numerous in both the lower and the upper surfaces. Their long axes lie in all directions. The hairs of the upper epidermis are simple, composed of two to five cells pyramided on a large basal cell which is surrounded by a cordon of large epidermal cells.

There are two layers of elongated cells in the palisade, which is rather loosely arranged with considerable air space, especially near the stomata. The cells of the mesophyll are more or less isodiametric, and arranged so as to provide for large air spaces in the vicinity of the stomata of the lower epidermis. They are compact around the bundles, forming a rather thick supporting sheath.

The bundles form an extensive network of veinlets through the mesophyll. They are bicollateral and undergo considerable secondary thickening. Figures 45-46 show transverse sections from the cotyledons, selected so as to show the general features described.

EPICOTYL

No extensive studies of the epicotyl were made other than to establish the nature of its vascular connections to the hypocotyl (fig. 32). There are usually six bundles in the epicotyl at the level where its first leaf diverges. These six bundles are branches from the six bundles of the hypocotyl, and have the same relative position with respect to one another and to the axis. In cross section they appear as two sets with three bundles in each set. One set of three enters the first leaf and the other set enters the second leaf. Branch-



FIGS. 45-49.—Figs. 45, 46, transverse sections of cotyledons: fig. 45 from central portion and fig. 46 at margin (*ep*, epidermis; *pal*, palisade; *msl*, mesophyll, *iph*, internal phloem; *px*, protoxylem; *mx*, metaxylem; *sec x*, secondary xylem; *e ph*, external phloem; *sto*, stomate; *hr*, epidermal hair). $\times 30$. Figs. 47-49, transverse sections of hypocotyledonary bundles showing origin of internal phloem: Fig. 47, transition bundle, at peg level, of five days old seedling (*l ph*, lateral phloem; *pi*, pith). Fig. 48 (from level just below cotyledon, same aged plant), internal phloem forming by divisions of pith cells. Fig. 49, same position as fig. 47 but of a nine days old seedling. $\times 27$.

ing of these six bundles of the epicotyl from the bundles of the hypocotyl occurs in the following manner. At or just below the level at which the cotyledons diverge from the axis, branch bundles to the epicotyl diverge from each of the four transition bundles. At this level the two remaining bundles of the hypocotyl have already branched preparatory to entering the cotyledons. Divergences to the epicotyl occur from each of these branches, and soon anastomose to form the bundles of the midribs of the first and second leaves of the epicotyl respectively. Cases occur in which these bundles of the midribs diverge as single strands from the corresponding bundles of the hypocotyl, before they branch to the cotyledons (figs. 37-41).

The divergences of the bundles to the epicotyl begin at a much earlier stage than that used for illustrative purposes. In fact their development is evident in seedlings whose hypocotyls have hardly emerged from the integuments. In such early stages, however, these nutritive connections between the axis and the epicotyl appear only as two arcs of undifferentiated, highly parenchymatous tissue lying in the zones where the actual vascular connections are to develop. Within these arcs of parenchyma again, the phloem differentiates before the xylem. The bundles are bicollateral from the beginning. It is only when the tissues of these new bundles have been well differentiated that the vascular connections to the epicotyl can clearly be determined.

When these bundles have definitely been established, a zone of tissue differentiates across the epicotyl between the two sets of bundles, and the first leaf soon diverges from the axis (figs. 32, 42-44).

Summary

1. Early stages of development of the watermelon seedling and its gross structure are described.

2. The primary root is tetrarch exarch. In transition each xylem strand is divided into two. These two divisions swing outward through arcs of 180° , and converge by pairs in front of the four phloem groups. When transition is completed there are four bundles composed of the four original phloem groups intact and of xylem which comes in approximately equal amounts from two adjoining

groups of xylem of the original alignment. The transition is rapid and is completed at the level of the peg.

3. There is one common histogen in the primary root; all primary tissues are derived from a common meristematic region.

4. The endodermis and inner cortical layers, as well as the pericycle, of the primary root contribute to the building up of the tissues of the secondary roots.

5. There are usually six bundles in the hypocotyl: the four transition bundles and two others which are anastomosed branches from the transition bundles. All these bundles diverge into the cotyledons.

6. For a considerable period of time the cotyledons serve as photosynthetic organs.

7. The epicotyl develops slowly at first, because its vascular connections with the axis are, in the main, differentiated after germination.

8. The bicollateral bundles extend from the level at which transition is completed upward through the hypocotyl into the cotyledons and into the epicotyl. The internal phloem is derived from the parenchyma which lies adjacent to the inner faces of the bundles. It does not extend into the roots, but is connected laterally with the external phloem in the transition zone.

JOLIET TOWNSHIP HIGH SCHOOL
JOLIET, ILLINOIS

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